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A Method for Estimating Marine Habitat Values Based on Fish Guilds, with Comparisons between Sites in the Southern California Bight

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A METHOD FOR ESTIMATING MARINE HABITAT VALUES BASED ON FISH GUILDS, WITH COMPARISONS BETWEEN SITES IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

Habitat valuation is an essential tool for tracking changes in habitat quality and in adjudicating environmental mitigation. All current methods for estimating habitat values of coastal marine sites rely heavily on the opinion of experts or on data variables that can readily be manipulated to influence the outcome. As a result, unbiased, quantitative comparisons between the values of different marine habitats are generally unavailable. We report here on a robust, objective technique for the valuation of marine habitats that makes use of data that are commonly gathered in surveys of marine fish populations: density, fidelity, and mean size. To insure comparability across habitats, these variables are assessed for guilds of fishes, rather than for single species. The product of the three guild-based parameters is transformed to its square root and then summed across all guilds in the habitat, yielding a single measure of habitat value for each site surveyed. To demonstrate the usefulness of this approach, we have analyzed data from existing surveys of 13 marine sites in the Southern California Bight, encompassing 98 fish species from 23 guilds. For seven of the sites, it was possible to develop estimates of the confidence interval of the habitat valuation, using a resampling technique. Variance estimates from resampling in one habitat mirrored those derived from analysis of annual variation. The resultant ranking of habitat types was: kelp beds > shallow artificial reefs > wetlands > protected shallow waters (soft bottom) > shallow open coastal sand (depth <30 m) > soft bottom habitat on the continental shelf (30 m < depth <200 m) > soft bottom habitat on the continental slope (depth >200 m). Although our data sets were restricted to Southern California, similar data could be obtained from any reasonably well-studied marine environment. The guild-based valuation technique may, therefore, be broadly applicable to the analysis of other marine ecosystems.

That natural habitats have an intrinsic value is one of the cardinal assumptions of the environmental sciences, and knowledgeable individuals usually concur on the relative ranking of the values of any two comparable habitats. A judgement of relative value is insufficient as a basis for environmental assessment, however. An explicit, objective measure is required to appraise the degree of environmental degradation in a local area or to track the course of recovery of protected ecosystems. Quantitative methods are also called for in adjudicating environmental mitigation. Since full recovery of a lost or degraded habitat is seldom feasible, the courts require an explicit determination of the degree of damage and the value of potential mitigating improvements.

It is seldom an easy matter to express habitat value as a single number that can be usefully related across a set of comparable habitats. This is particularly true in the marine environment. Such measures as the U.S. Army Corps of Engineers' (1984) reference to ratio (RTR) technique or the U.S. Fish and Wildlife's (1980, 1981) habitat evaluation procedures (HEP) and habitat suitability indices (HSI) have rarely been used in marine habitats, because the necessary data are seldom available. As a result, valuation of marine

habitats has commonly fallen back on "best scientific judgement" as a means of filling in the gaps in the data.

In this paper, we describe a novel, alternative approach to habitat valuation that makes use of data that are commonly collected in surveys of marine habitats. The technique is based on measurements of fish guilds, rather than individual species. Limiting the scope of our data to fishes is not intended to downplay the importance of other members of the community. But we felt that the fish assemblage is a good indicator of the health of the entire community, and the ease with which fish species can be recognized in the field makes fish an inexpensive source of comparison, and one that can be acquired rapidly. Our use of guilds serves to enable comparability across habitats, as many fish guilds are found in a large number of differing habitats. Individual species are subsumed into larger ecological categories, to avoid the inherent arbitrariness and potential bias of examining only "key" species. Subjectively weighting our model with the relative import of key economic, ecological or perhaps endangered species was not attempted. We acknowledge that the perceived relative worth of these species will change over time and between interest groups. Fish guilds based upon community, feeding technique, activity period and refuge location (M. J. Allen, 1982) were established a priori to the analysis. In our approach, measures of the abundance, fidelity, and mean length of fish in each of 23 guilds are cumulated to obtain a numeric estimate of habitat value. The more guilds that are represented in a given habitat and the greater their abundance and reliability, the higher the valuation of the habitat.

We have illustrated the technique using data drawn from existing surveys and tables in the literature for 13 sites in the Southern California Bight. The guild-based valuation model was, however, designed to be broadly applicable to other marine ecosystems, as well. Similar comparisons could be produced inexpensively from long-term surveys of any reasonably well-studied area. Our technique should, therefore, provide a valuable tool for tracking the state of marine ecosystems and determining mitigation in the marine environment.

Methods

Data Sources.—To develop our analytical technique, we conducted an extensive review of prior studies from the Southern California Bight, searching for data sets with repeated samples over a series of years and all seasons. In the end, we selected thirteen habitats from the studies available (Fig. 1). Seven of the habitat sites were designated as "primary," in that they had been surveyed by the Vantuna Research Group (VRG) over the course of as much as 20 yrs, resulting in a large and detailed data base of observations. The primary sites included five areas sampled exclusively with otter trawls: Los Angeles Harbor, Shallow Sand (depth <30 m), Continental Shelf (30 m ≤ depth < 200 m), White's Point Outfall (depth = 60 m), and Continental Slope (depth ≥ 200 m). The Shallow Sand, Continental Shelf and Continental Slope sites are composites of trawls conducted from below Port Hueneme, Ventura to Carlsbad, in a continuous time series between 1974 and 1996 (Love et al., 1986). The two remaining primary sites were reef areas sampled with visual SCUBA transects and ichthyocides: King Harbor at Redondo Beach, and the kelp bed at Palos Verdes Point, Rancho Palos Verdes (Stephens and Zerba, 1981; Stephens et al., 1984, 1986, 1994).

Six additional, "comparison" sites were evaluated on the basis of data in the existing literature or in other, smaller research data bases. The comparison sites included a second study of the White's Point outfall area from otter trawl data made available by the Los Angeles County Sanitation district (LACSD) and data from the Marine Review Committee's analysis of San Onofre Nuclear Generating Station (SONGS) including both SCUBA transects of the kelp bed, and shallow otter

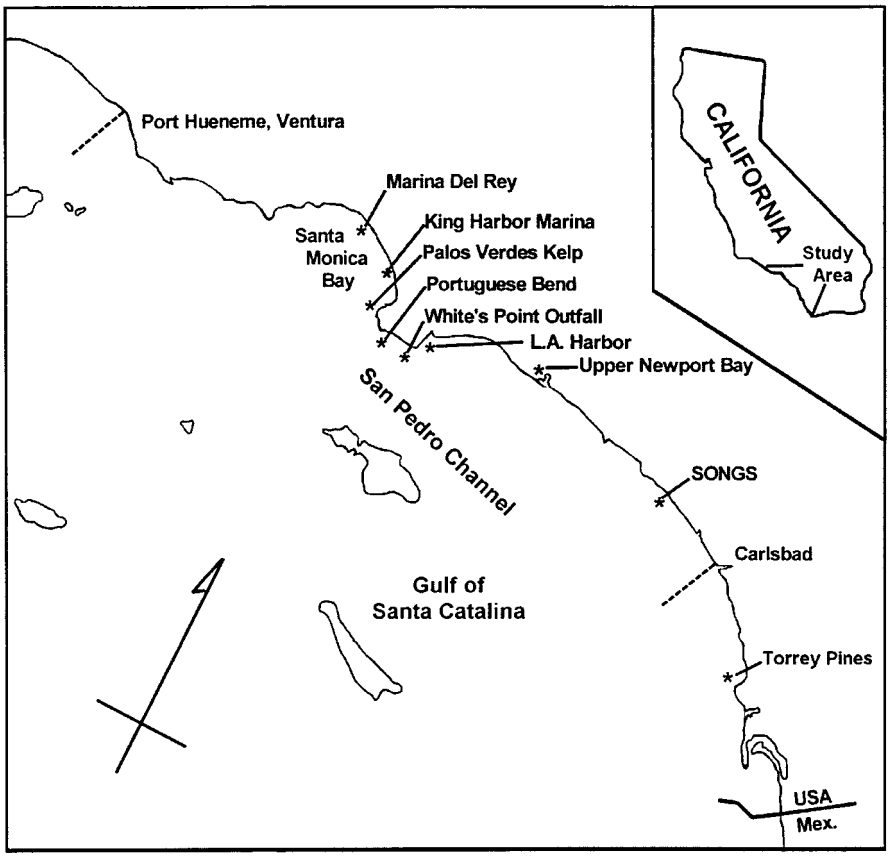

Figure 1. Map of the study sites in the Southern California Bight used for habitat valuation. Primary sites include Los Angeles Harbor, Shallow Sand, Continental Shelf, White's Point Outfall, Continental Slope, King Harbor, and Palos Verdes Kelp. The Shallow Sand, Continental Shelf and Continental Slope stations are composites of trawls from Port Hueneme, Ventura to Carlsbad, demarcated to the north and south with hatched lines. Comparison study sites included a second data set from the White's Point Outfall, data from the analysis of the San Onofre Nuclear Generating Station (SONGS), and studies of Upper Newport Bay, Mother's Beach, Marina Del Rey, and Portuguese Bend.

trawls and lampara nets in the adjacent shallow sand area. A study of Upper Newport Bay, Newport Beach (L. G. Allen, 1982) conducted with beach seines, common sense seines, and drop nets with quinaldine; a study of the Torrey Pines artificial reef (diver transects, traps, etc.) (MEC, 1991); and the VRG studies of Mother's Beach in Marina Del Rey (beach seine only; Stephens et al., 1992) and the marine area proximate to the Portuguese Bend landslide (otter trawl, beach seine, divers transects, and ichthyocides) conclude the list. The VRG primary site database includes repeated samples since the early 1970s and may include more than 20 yrs of data per site. The LACSD data set is also long-term. Other data sets usually cover less than 2 yrs but include multiple samples.

Kelp beds and associated rocky reef habitats were compared at three sites: Palos Verdes Point, San Onofre and Portuguese Bend. Portuguese Bend is a rocky reef area impacted by a landslide. Artificial habitat comparisons were based on two sites, King Harbor and Torrey Pines. We used the data from Newport bay and Marina del Rey to examine wetlands. The remaining locations examined soft bottom habitats.

Sampling Methodology.—Abundance estimates of marine fish depend upon and differ among sampling methods and no single method is equally successful for all species. For soft substrates, the

most readily available data come from otter trawls, which have been used regularly within the Southern California Bight since the early 1970s (Mearns and Stubbs, 1974: Mearns and Allen, 1978). This method captures fish associated with the substrate, but does not adequately sample the water column above. Lampara or purse seines are the best quantitative measures of fish in the water column, though gill nets supply a qualitative measure of available species. For hard substrates, including artificial reefs, natural reefs, and kelp beds, diver transects as well as quinaldine or rotenone stations, traps, or gill net data are commonly available. In very shallow waters, such as sand beaches or bays and estuaries, beach seines, meter square pumped samples, or traps have commonly been used.

Most sampling techniques for marine fish are not particularly efficient, in that they do not provide a complete description of the local community (Stephens, 1978; MEC ,1988; Davis and Anderson, 1989). To avoid this problem, individual sites in Southern California have often been surveyed using several different methods. Where multiple data sources were available, we have attempted to derive density estimates that make use of the best features of each of the techniques employed. If there was little overlap between methods, in terms of the occurrence of particular species, we summed densities across methods. If the species overlap was large, we selected data from the highest density estimate for each species.

TRAWLS.—Interpretation of trawl data presents several technical difficulties. To obtain fish densities from trawl surveys, we needed to compute the area sampled, which required knowing the trawl width and the distance traveled. Trawls are commonly compared by estimating bottom time, that is, the time between termination of net payout and initiation of retrieval. The product of bottom time and vessel speed should provide the best indirect estimate of distance traveled, though more recent technologies (Loran or Global Positioning Systems) could, of course, yield a more accurate measure. With the exception of very shallow trawls, however, the actual bottom time is not accurately reflected by the difference between payout and retrieval. Because of lags introduced by water resistance, the net does not contact the substrate until sometime after the cable has been fully paid out; it also does not leave the substrate immediately upon initiating retrieval. The lag times vary systematically with depth and are affected by vessel speed and currents. As a result, there is a significant, inherent inaccuracy in trawl data that makes them difficult to compare to other assessment techniques.

To compensate for the error in estimating tow area, we conducted a series of calibration tows, sampling at a range of depths between 55 and 183 m with both 4.9 and 7.6 m head rope nets. The calibration tows were monitored with a Wildlife Computers microprocessor-controlled time-depth recorder, model MK3e, that enabled us to measure time on the bottom accurately. We developed a correction function for bottom time for each net size that was subsequently applied to all VRG trawl data from the primary sites. The second component of the area sampled by trawling, trawl width, has previously been dealt with in the literature. Most trawl surveys in Southern California (Mearns et al., 1973; Stephens et al., 1973, 1974; DeMartini and Allen, 1984; Mearns et al., 1980) have used 4.9 or 7.6 m head rope nets, and Mearns and Stubbs (1974) estimated trawl widths for nets of this dimension. Larger nets provide a larger, and therefore more accurate, sample of substrate fauna than smaller ones, but we have no data that would allow us to make a correction for this variable.

The correction function for bottom time was also applied to trawl surveys in the comparison site data, where it was feasible. DeMartini and Allen (1984) estimated distance with a Miniranger and spar buoys for their trawl data at SONGS. We accepted these as accurate trawl distances, since all of these trawls were shallow. Except for very shallow studies, no estimate of fish abundances from the water column was available. Allen and DeMartini (1983) sampled the shallow water column with lampara nets, enabling us to combine the lampara data with their trawl study in evaluating the SONGS soft substrate site. The Portuguese Bend study sampled the nearshore water column with beach seines as well as trawls.

DIVER TRANSECTS.—Diver transect data sets usually include density calculations and are, therefore, readily comparable. The studies of King Harbor and the kelp bed at Palos Verdes Point (Stephens and Zerba, 1981; Stephens et al., 1984, 1986, 1994) and San Onofre (Larson and DeMartini, 1984)

included both bottom and water column transects, though the published data from the latter survey appear to include only selected species. VRG data from King Harbor and Palos Verdes were accompanied by m^2 bottom samples that were poisoned with quinaldine to assess the abundance of cryptic fish. Allen et al. (1992) presented similar data for Catalina Island. We added their estimates of cryptic fish to the San Onofre kelp data set, correcting for the proportion of hard substrate, to render the two kelp bed studies more comparable. The study of Torrey Pines artificial reef includes all relevant data parameters (MEC, 1991). The principal weakness of diver transect data is a lack of measured fish lengths or weights. Larson and DeMartini (1984) published approximate mean length or weight for different age classes of the study species at San Onofre. We used these data for the mean length component of our habitat valuation of diver transect sites, supplemented by additional estimates for species not included in their list.

WETLANDS.—There have been very few quantitative, multiple-sample studies of fish assemblages in Southern California wetlands. Allen's (1982) survey of upper Newport Bay is the most complete, and we used it as the principal source of data for characterizing this habitat. Although it is not a complete sampling regime, we used the long-term VRG study of Mother's Beach in Marina Del Rey (Stephens et al., 1992) as an additional comparison, because this appears to be the only other suitable data set available.

GUILD DEFINITIONS.—Because our measure of habitat value is based on guilds, rather than individual species, it was necessary to settle on a listing of fish guilds and characteristic species that would apply to all 13 habitats in the study. Our guild classification (Appendix A) is a modification of Allen's (1982) taxonomy, which separates species by communities (i.e., surface, water column, substrate associated, or benthic), as well as preferred foraging location, feeding technique (filter, selective, pickers, engulfers, etc.), activity period (nocturnal or diurnal), and location of refuges. We chose to include the broadest possible array of guilds, as a means of enhancing the sensitivity of our measure and avoiding evaluative biases for or against particular habitats. Where species undergo ontogenetic changes from one guild to another, they were distributed between the guilds by the size at which they switch. We used fidelity as the criterion for selecting species to be included in the analysis, accepting all species that occurred in any of the study habitats in at least 25% of the samples.

DATA TRANSFORMATIONS.—Data from all sources were converted to daily assays and the records pertaining to species in the guild structure were extracted. For each species, density was expressed as abundance per hectare, fidelity as percent daily occurrence (a fraction between 0 and 1), and length as standard length in mm.

TRAWL DATA.—For otter trawl data, we first calculated the area of each tow, as described above. Records of species that were not included in our guild listing were deleted. The remaining records were then condensed, producing a single record for each age (length) class for each species for each tow. (Because nine of the 98 species in our guild listing were categorized into different guilds as juveniles than as adults, both species identification and age status had to be retained.) To enable us to compute mean length within species or guild categories, these records carried along both abundance and the product of abundance and length (the "length product"). We pooled the results of all tows within habitats, producing a single record for each survey day. These daily records were then used as the basis for computing abundance, fidelity, and mean length for each of the 107 species/age categories in the guild listing.

For each habitat, we calculated the category densities by cumulating all counts for each category and dividing by the total area surveyed in that habitat. Reasoning that absence from a small tow should have less influence on the fidelity estimate than absence from a large one, we weighted our estimate of fidelity within species/age categories by the area covered in each day's survey. Thus, the fidelity for each category was the ratio of the sum of the areas surveyed on days in which the species was encountered to the total area surveyed in the habitat for all sample days. To calculate mean length, the sum of the length products over all daily records for a given category was divided by the sum of abundances. The category estimates were then summed within guilds.

Guild densities were simply the sum of the densities of the individual species making up the guild. Mean length was weighted by relative abundance and calculated as the sum of the length products for each species within the guild divided by the aggregate abundance for the guild. Although guild fidelity could have been calculated directly from the raw data for the primary sites, the sources for many of the comparison sites precluded such simple treatment, as they had already computed fidelity by species. To maintain consistency, therefore, we used an indirect approach which involved the combining of species fidelities into guild fidelities for all 13 sites. To calculate guild fidelity, we made the assumption that the probability of occurrence of one species in a habitat was effectively independent of that of others within the guild. That is, we assumed that there was no competitive exclusion between different species in the same guild and habitat. Given this assumption, the probability that no members of a given guild will occur in a daily survey of a given habitat is the product of the non-occurrence probabilities of each of the species within the guild. If FA is the fidelity of species A, expressed as a ratio between 0 and 1, the estimated fidelity for a guild made up of species A, B, and C would be G, where (1-G) = (1-FA)*(1-FB)*(1-FC). Values for guild density, fidelity, and mean length were computed for each of the five primary habitat sites that were based on trawl data. We handled the data from Los Angeles County Sanitation District in a similar fashion, but because no fish measurements were included, we substituted mean lengths for each species calculated from the VRG database.

Diver Transect Data.—For diver transect data at King Harbor, the process was simplified, because each transect covered a constant area (150 m^2). In the data base, individuals were categorized as juvenile, subadult, or adult. Mean size data from published listings (Larson and DeMartini, 1984) for each of these life stages were used to estimate length of observed individuals. As in the trawl studies, we then aggregated the data within sampling days, combining observations of subadults into the adult age category. A similar analysis was performed on the cryptic fish data obtained from rotenone and quinaldine poisoning, but poisoning stations differed in area and included length measurements for all species. To combine the transect and cryptic fish data sets, we generated two species/age category tables, one from each source, and ensured that there was no species overlap. That is, species that occurred in both data sets were retained in the set that was independently assessed to provide the best estimate of its density and deleted in the other. The two data sets were subsequently combined, and guild-based estimates were derived in essentially the same fashion as was used in processing the trawl data.

The Palos Verdes survey included three separate components: rock substrate transects at 3, 6, 9, and 12 m, kelp canopy transects at 3, 6, and 9 m, and cryptic fish samples from poisonings of 1-m^2 quadrats. Equal numbers of transects were run at each depth in both the rock and kelp components. To combine the rock and kelp substrate data, we weighted the kelp canopy surveys in accordance with their contribution to an idealized reef face. That is, the 3-m canopy transects were weighted by 3, since they occurred above the 6, 9, and 12-m rock transects, and the 6-m canopy transects were weighted by 2 because they occurred only above the 9 and 12 m transects. The combined data represent the density of each species over a 960 m^2 cross-section of the reef, in which the water depth varied between 3 and 12 m. Daily fidelities were calculated separately for rock and canopy transects and combined using the product of the non-occurrence probabilities by species. Age designations and cryptic fish were handled as in King Harbor. Mean size calculations were simply the product of mean size and abundance (all areas) divided by total abundance.

Other Data Sources.—Most of the comparison site data were taken from published literature. As no information about fidelity was included in the SONGS data, calculation of site-specific species occurrence by day was subsequently made available to us from the primary SONGS database by Southern California Edison Co. None of the studies from published data included more than two years of work. Habitat values generated from these data are, thus, necessarily less robust than those produced from the primary site data.

Determination of Habitat Value.—Our initial data extraction yielded measures of density, fidelity, and mean length for each of 23 guilds in seven basic habitat types: rocky kelp reefs, artificial reefs, harbor soft substrate, shallow sand, shelf soft substrate, slope soft substrate, and back bay

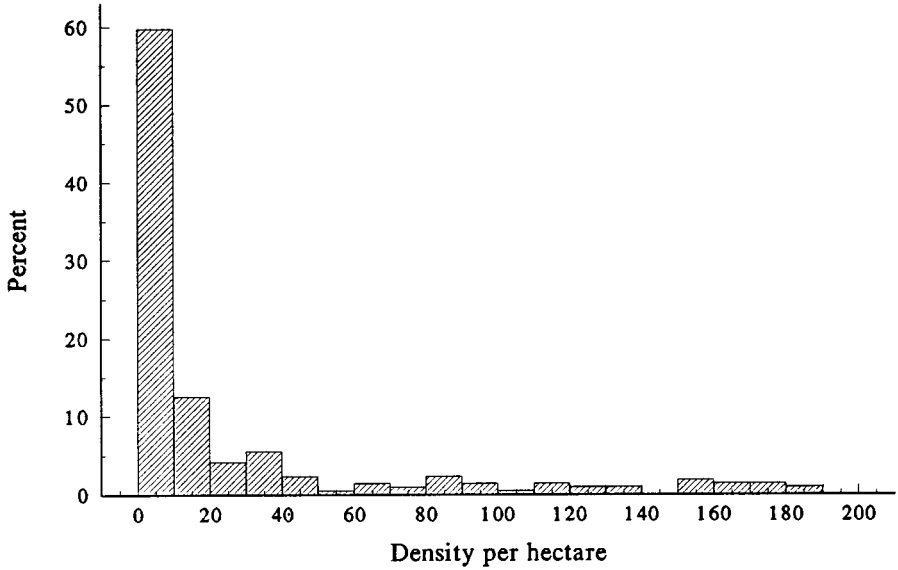

Figure 2. Histogram of guild densities, pooled across 16 data sources, a total of 368 data points. The distribution is displayed in truncated form to improve visualization: the maximum guild density in these data sets exceeds 170,000 ha^{-1}.

wetlands. In addition, we had measures from two sites that have been subject to potentially degrading environmental impacts: the Los Angeles County Sanitation District sewage outfall at White's Point and the Portuguese Bend slide habitat. We then combine these measures into habitat values that would allow direct comparisons between sites.

We did not consider the three measured components as being of equal importance in determining habitat value. Density was viewed as being central to the issue, while length and fidelity were secondary factors that mainly served to adjust for anomalies in the abundance measure. Presumably, we could have normalized each of these variables across all habitats and combined the scores as a weighted sum, but such an approach is inherently arbitrary and dependent on the choice of weights and transformation functions. The simplest alternative was the product of the three parameters. It did not require arbitrary weightings, it was independent of the particular habitats that were included in the comparison, and it had a direct, physical interpretation: it was simply a measure of aggregate fish density corrected for variance in the occurrence of species over time and weighted by mean length.

To examine the statistical features of this estimator, we generated histograms from the individual guild measures pooled from the 16 data sources listed in Tables 1 and 2. When zero-abundance guilds were eliminated, there were a total of 271 data points. Guild density (Fig. 2) shows a clear preponderance of low densities, with an extremely long tail, indicating very high densities for a few guilds in some habitats. This compound Poisson distribution is often seen in abundance data from natural communities (Pielou, 1969). Fidelity (Fig. 3) also shows a modal peak at the low end of the scale, but the remainder of its distribution is fairly uniform, and mean size (Fig. 4) appears to be nearly log-normally distributed.

A correlation analysis of the three measures showed that density and fidelity were wholly independent ($r < 0.004$), while mean length was marginally negatively correlated with each of the other two variables ($r \geq -0.12$). Large fish appear to be rarer and less reliably present than small fish, but the correlations with mean length failed to achieve statistical significance. A multivariate regres-

Table 1. Square root products for each of the 23 guilds from the seven principal study sites. The sum of the product measure across guilds constitutes the value of the given habitat. Table also displays statistics from a 1000-iteration resampling analysis of these data bases, showing mean, median, and 95% confidence limits of the median. Shallow (<30 m), Shelf (30–200 m), and Slope (>200 m) sites are composites of otter trawls conducted between Port Hueneme, Ventura, and Carlsbad. For exact station locations, see Figure 1. All data bases were acquired and maintained over a 20-yr period by the Vantuna Research Group.

Guild	Hard Substrate			Soft Substrate			
	Palos Verdes	King Harbor	LA Harbor	Shallow	Shelf	Point	Slope
1	0.0	74.9	52.9	62.5	1.7	3.5	0.2
2	32.6	51.3	127.3	129.4	1.1	0.1	0.1
3	6.1	89.8	109.0	132.1	4.1	0.1	0.0
4	446.0	178.9	0.6	0.7	0.2	0.1	0.5
5	687.1	608.2	9.4	2.1	30.0	33.7	11.8
6	23.6	43.7	0.4	0.6	34.3	50.5	46.3
7	0.0	0.0	9.4	9.3	52.8	38.7	23.9
8	847.8	302.3	8.6	7.9	2.8	4.7	0.0
9	465.0	301.0	5.3	14.0	0.1	0.0	0.1
10	11.9	36.2	2.6	8.6	37.1	39.1	1.3
11	257.6	305.0	42.3	25.4	12.6	9.3	0.5
12	316.1	235.3	1.2	4.0	0.4	0.1	0.0
13	509.4	247.8	0.0	0.1	0.0	0.0	0.0
14	63.2	168.8	173.5	131.3	40.8	20.4	2.3
15	0.0	0.1	1.7	6.4	11.3	16.0	6.5
16	8.2	30.0	48.2	33.4	15.0	16.9	1.9
17	10.5	35.8	31.9	35.1	100.2	92.0	67.1
18	524.3	319.4	0.6	1.2	2.6	2.2	26.6
19	1,131.5	884.2	0.3	0.3	0.0	0.0	0.0
20	250.4	303.2	0.1	0.4	0.1	0.0	0.0
21	0.0	0.0	69.6	10.2	21.9	22.4	37.0
22	2.0	22.3	23.9	30.6	91.2	102.5	79.3
23	160.8	201.3	1.0	5.2	0.2	1.6	0.2
Value	5,754.1	4,439.5	719.6	651.2	460.4	454.1	305.6
Bootstrap Results							
2.5% (low)	5,276.3	4,218.5	637.9	618.5	412.7	408.5	273.0
mean	5,438.5	4,606.7	709.5	649.9	458.0	449.8	304.6
median	5,437.7	4,613.9	710.6	650.0	458.1	449.9	304.5
97.5% (high)	5,606.0	4,995.3	781.0	677.5	501.0	492.1	334.2
sample days	158	200	110	259	202	212	137

sion of the three-parameter product on density, fidelity, and mean length showed that fidelity accounted for 15% of the variance in the product, density for 13%, and mean length for 2.6%.

Because of the highly skewed distribution of densities, the distribution of the product of the three parameters is also highly skewed (Fig. 5). This has the undesirable consequence of emphasizing abundance, at the expense of ecological diversity, as the basis for judging habitat quality. If we determine the number of guilds at each site for which the density was greater than five fish per hectare, we get a measure that varies between 5 and 18 across the 16 data sources in our survey and constitutes a rough estimate of community diversity. The consequence of the high positive skew in

Table 2. Square root products for each of the 23 guilds from the six comparison sites, arranged by data source and location. The sum of the product measure across guilds constitutes the value of the given habitat. Locations are: Los Angeles County Saniation District (LACSD) trawls of the White' s Point outfall (60 m); San Onofre Nuclear Generating Station (SONGS), including the nearshore surveys by DeMartini and Allen using lampara and trawls and Larson and DeMartini' s study of the San Onofre kelp bed; Marine Ecological Consultants (MEC) study of Torrey Pines artificial reef; Allen' s study of Upper Newport Bay; and the Vantuna Research Group' s (VRG) studies of Mother's Beach in Marina del Rey and the Portuguese Bend area near Palos Verdes.

Guild	LACSD Outfall	SONGS Lampara	SONGS L&T Combined	SONGS Trawls	SONGS Kelp Bed	Torrey Pines	Newport Bay	Marina del Rey	Portuguese Bend
1	4.1	300.8	300.8	0.0	0.0	0.0	249.0	5.0	464.8
2	14.5	84.6	84.6	95.1	0.0	0.0	887.1	1,190.9	173.1
3	1.8	88.0	88.0	58.1	0.9	3,303.0	3.0	0.0	88.7
4	0.0	55.8	55.8	0.0	46.2	0.0	1,845.4	578.5	58.3
5	48.3	0.0	0.0	0.0	1.1	1,086.9	0.0	0.0	13.0
6	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
7	46.5	0.1	16.2	16.2	0.0	0.0	3.8	0.0	11.8
8	11.6	1.0	9.7	9.7	581.1	676.1	658.6	152.4	0.0
9	2.4	2.2	7.8	7.8	329.9	588.4	0.0	44.6	30.6
10	34.8	1.1	6.4	6.4	0.0	185.5	0.0	0.0	18.3
11	19.5	5.9	64.0	64.0	86.4	901.6	0.0	0.0	15.7
12	1.8	0.0	0.2	0.2	282.8	597.6	0.0	0.0	0.0
13	0.2	0.3	0.3	0.0	118.3	277.7	4.2	0.0	0.0
14	14.7	105.4	105.4	135.6	3.3	306.1	2.6	88.2	50.2
15	4.5	0.7	128.1	128.1	0.0	0.0	0.0	0.0	0.0
16	33.3	3.6	41.0	41.0	0.0	102.5	4.5	7.4	69.5
17	103.4	0.4	149.5	149.5	0.0	18.9	0.0	0.0	85.9
18	9.7	0.0	0.3	0.3	0.0	0.0	120.2	33.6	0.0
19	0.1	0.0	3.1	3.1	0.0	546.6	202.9	69.6	0.0
20	0.1	0.0	0.0	0.0	0.0	21.8	0.0	2.5	0.0
21	36.5	0.0	46.3	46.3	0.0	0.0	3.1	0.0	60.7
22	115.2	1.2	51.2	38.7	0.1	46.5	18.6	78.5	47.5
23	0.2	68.5	68.5	0.0	139.4	0.0	2.5	163.5	0.0
Value	553.0	719.7	1,227.2	800.1	1589.5	8,659.2*	4,005.4	2,414.5	1,188.0

*this value is anomalous and its adjusted value is 2589 (please see discussion)

the three-parameter product is a relatively low correlation between the product, averaged across the 23 guilds at each site, and this measure of number of guilds. Only 12% of the variance in the number of guilds could be accounted for by variation in the mean three-parameter product (r^2 = 0.12, P = 0.21).

To produce a more equitable weighting of diversity and abundance, we sought a transformation of the three-parameter product that would improve its correlation with the number of guilds and bring the contribution of each guild to the habitat totals closer to equality. We tested log, square root, and cube root transforms. Log transformation overcorrected the bias: The mean log product accounted for 84% of the variance in guild numbers, suggesting that the log transformation virtually converts the habitat sums to a linear function of the number of guilds. The square root and cube root transforms both generated significant correlations, accounting for between 33 and 47% of the variance in guild numbers. By this criterion, either would provide a suitable basis for a habitat value index. However, the range compression produced by the cube root transform seemed excessive. The coefficient of variation across guilds and habitats was 1.60 for the raw, three-parameter product,

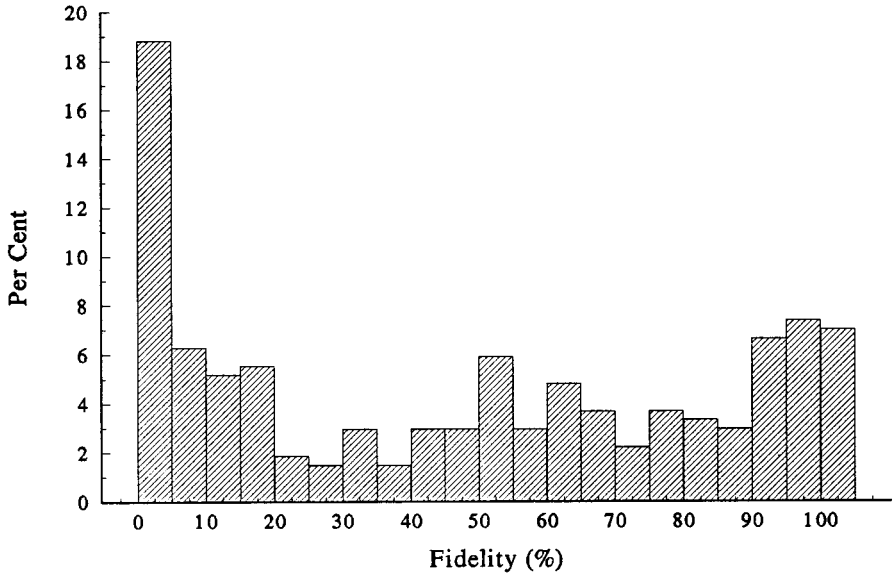

Figure 3. Histogram of guild fidelities for 23 guilds, pooled across 16 data sources. Note the modal bin at low fidelity values.

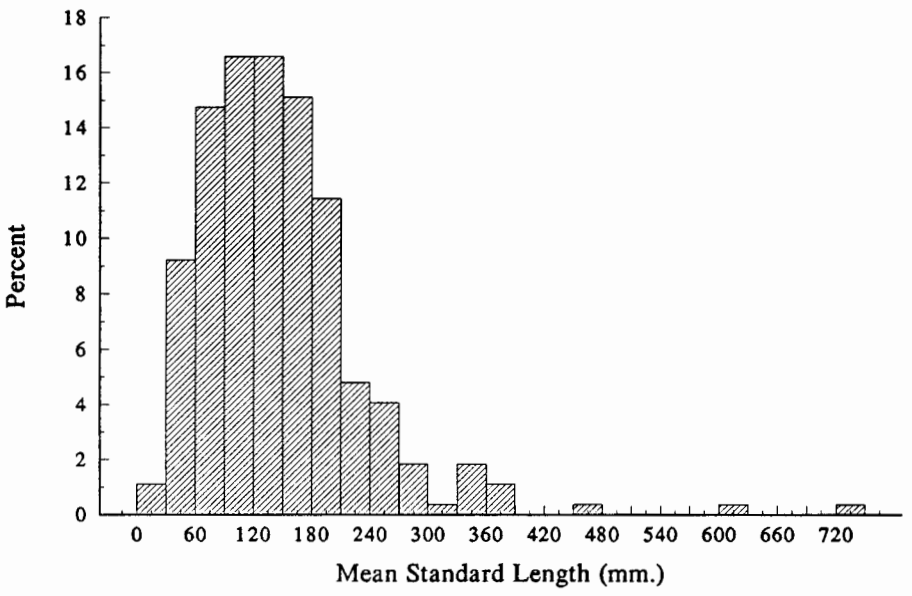

Figure 4. Histogram of mean sizes for 23 guilds, pooled across 16 data sources. Note the modal bin at low mean sizes.

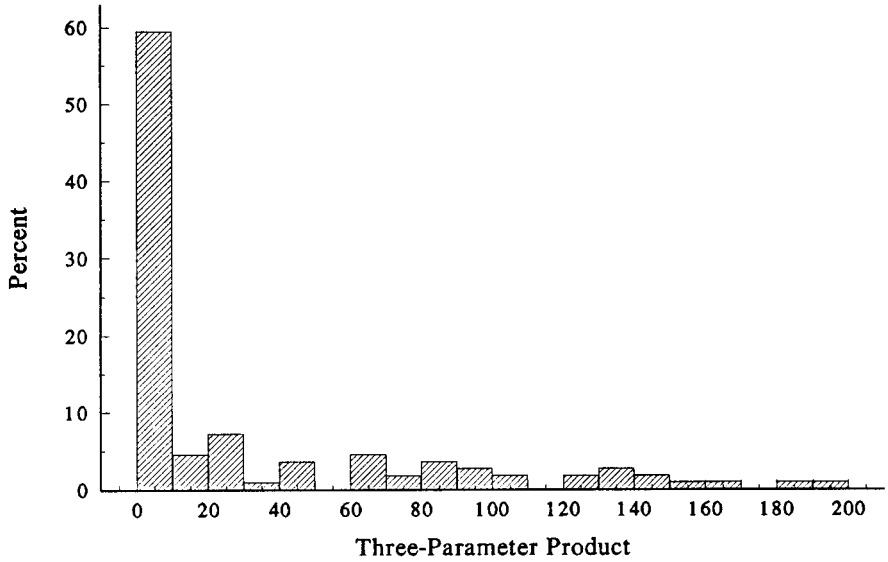

Figure 5. Histogram of the three-measure product for each of 23 guilds, pooled across 16 data sources. The distribution is displayed in truncated form to improve visualization: the maximum value in these data sets was over 1,625,000.

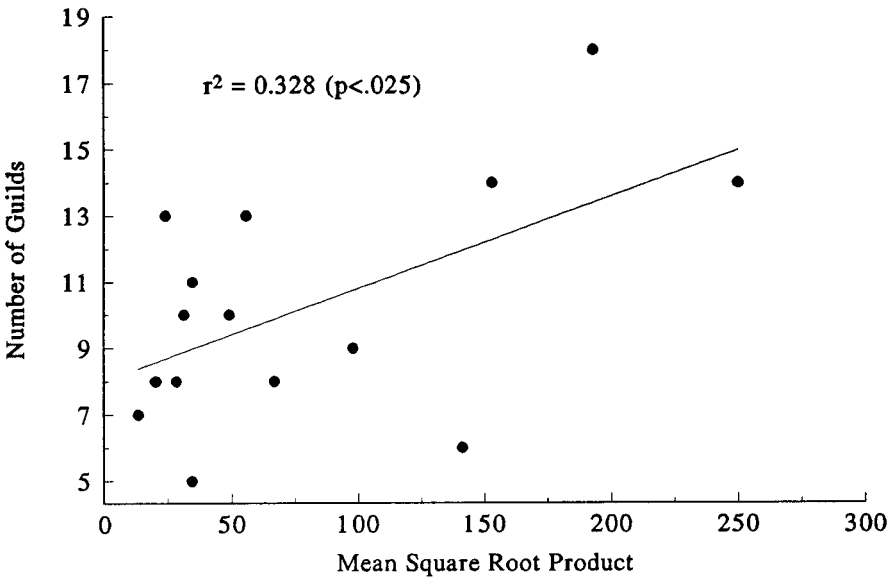

Figure 6. Number of guilds as a function of the square root of the three-parameter product. Points are mean values across guilds for each of the 16 data sources.

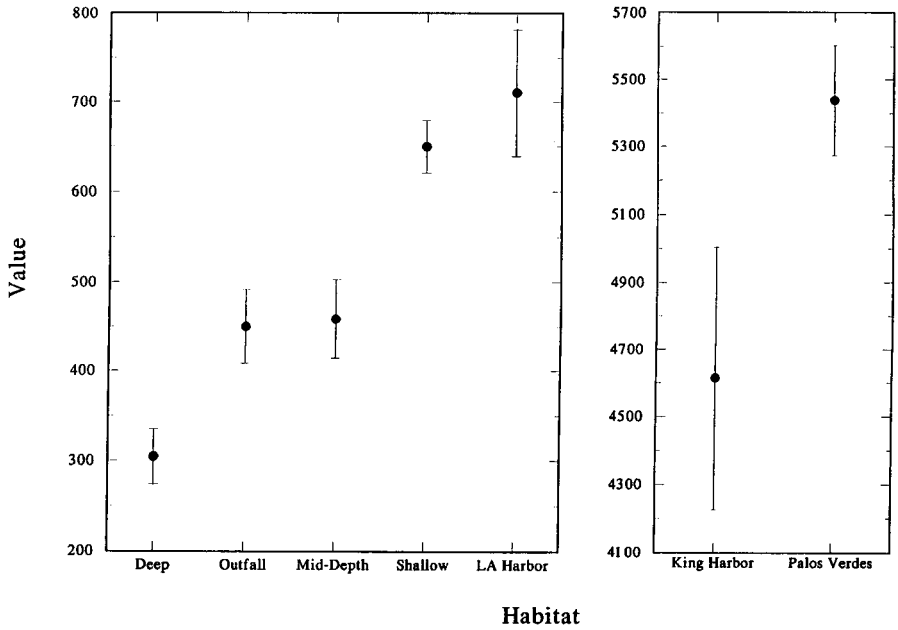

Figure 7. Resampling analysis of habitat value. Medians and 95% confidence limits from 1000 iterative samples of daily survey results for the seven principal sites.

0.80 for the square-root product, and 0.53 for the cube root product. The cube root significantly reduced the differences between habitats and, thereby, reduced the sensitivity of the measure.

We therefore settled on what is perhaps the conceptually simplest and most conservative transformation: the square root function. When the three-parameter product is converted to its square root, the transformation decreases the median by over an order of magnitude, from 937 to 31, but the effect on the range is far more dramatic: the highest value drops from 1,630,000 to 1275. This reflects about a 50% reduction in the skewness of the distribution of the habitat quality measure (from 6.0 to 3.34). The reduction in skewness greatly improves the relationship between the measure of habitat value and the number of guilds per site (Fig. 6). The r^2 for this regression is 0.33, significant at $P < 0.025$, indicating that the value measure accounts for about one-third of the variance in number of guilds, a much more acceptable outcome.

Calculation of Confidence Limits.—To calculate confidence limits for our measure of habitat value, we conducted a bootstrap analysis of the sites in the primary data set (Shao and Tu, 1995: Good, 1994). The bootstrap approach involves iterative computation of a statistic based on random subsets of the data available. When the computation is repeated hundreds or thousands of times, the resulting distribution of parameter estimates across the population of subsamples constitutes an objective, empirical sampling distribution of the underlying statistic. From this distribution, we can extract a measure of both the central value and the confidence limits of the statistic. Applying this methodology to our habitat value measure, we obtained the guild density, fidelity, and mean length for each survey day in the primary data set. At each site, a random half of the survey days were selected, the habitat value was estimated based on these data, and then another random selection was made. After 1000 iterations of selection and estimation, we obtained an empirical distribution of habitat value estimates for each site, from which we computed the median and 95% confidence limits. For King Harbor, we also obtained an independent estimate of variance by calculating the habitat value within each year's data for each of 10 yrs of the study.

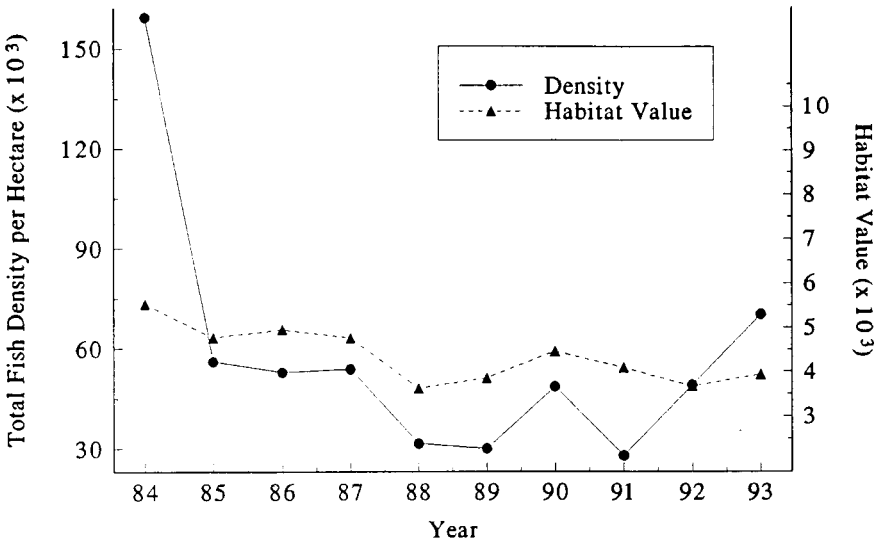

Figure 8. Habitat value and total fish density, computed within yearly intervals on data from the King Harbor artificial reef. Ordinates have been scaled in proportion to the variable means. Note that although the fluctuations in density are more extensive than those in habitat value, the value measure tracks, to some degree, yearly changes in fish density.

Results

Comparisons Among the Principal Sites.—For the seven principal study sites, Table 1 displays the square root of the three-measure product for each of the 23 guilds, along with the sum across guilds, which constitutes the aggregate value of the given habitat. These results are single estimates based on all of the information in the data set, which ranges between 110 and 259 survey days per site. Based on this analysis, the Palos Verdes natural kelp reef ranked as the most valuable site, followed by the King Harbor breakwater, a shallow, high relief artificial reef without kelp. Values for the five soft-substrate habitats were considerably lower, with the protected area behind the breakwater in Los Angeles Harbor ranking highest, followed by open coastal Shallow Sand, Continental Shelf soft substrate, White's Point outfall, and Continental Slope soft substrate.

The median and confidence limits for habitat values from the bootstrap analysis of these sites are displayed in Figure 7. The relative habitat values resulting from the bootstrap were virtually identical to those obtained using the full data set. If we recode the full data set values by dividing by the highest value obtained (the Palos Verdes reef), the remaining site values are 0.86, 0.14, 0.13, 0.09, 0.09, and 0.06, in the order of their listing in the previous paragraph. The same recoding procedure applied to the bootstrap medians produces relative site values of 0.85, 0.13, 0.12, 0.08, 0.08, and 0.06. It appears, therefore, that deriving the bootstrap estimates from random halves of the daily survey data did not introduce a systematic bias. The bootstrap confidence limits also appear to be in line with those obtainable from more conventional statistical approaches. The 95% confidence limits of the median estimated by the bootstrap technique bracket a range that is at most 20% of the site medians. When habitat value was measured within yearly intervals over a ten-year survey of King Harbor reef (1984–1993; Fig 8), the 95% confidence

limits spanned 18% of the mean, clearly indicating a comparable estimate of the reliability of the central measure. This provides a substantial assurance of legitimacy for inferences based on the bootstrap approach.

Based on the results of the bootstrap procedure, the White's Point sewage outfall site displays a habitat value that is centrally located within the confidence limits of the Continental Shelf soft substrate (Fig. 7), suggesting that the outfall does not differ significantly in value from other areas of similar substrate type and depth. The only other overlapping confidence limits in the analysis of the primary sites were shown between the Los Angeles Harbor soft substrate and the Shallow Sand habitat, another case of similarity in both depth and substrate type. The mean habitat value over all soft substrate sites, regardless of depth, was 514.4, compared to the mean for the two hard substrates of 5022.6, suggesting that a natural, high-relief rock reef with kelp (Palos Verdes) or a mature artificial reef (King Harbor) is roughly an order of magnitude more valuable than any comparable area of soft substrate habitat.

Contrasts Between Primary and Comparison Sites.—The data sets for the comparison sites (Table 2) were not subjected to bootstrap analyses, because, with the exception of the Los Angeles County Sanitation District (LACSD) trawls and the VRG Marina Del Rey site, they were drawn from surveys from no more than two successive years, limiting variation in habitat value. We can, however, compute habitat values from the data available in these studies and contrast them qualitatively with those obtained for similar habitats among the primary sites. The LACSD trawl surveys in the area of the White's Point outfall and the SONGS trawls both yield calculated habitat values that are higher than the values from comparable sites in the primary data set, but of similar orders of magnitude (553 vs 454 for the outfall sites and 800 vs 651 for the shallow sand sites, respectively).

The SONGS trawl and lampara data sets can be combined, providing an improved measure of the value of shallow soft substrate habitat that includes the water column as well as associated benthic fauna. This synthesized shallow habitat yields a value of 1227, about 30% higher than that provided by the shallow sand otter trawls alone. The VRG samples from Portuguese Bend on the Palos Verdes peninsula also sampled a shallow water column, in this case with beach seines. Fifty years ago, this site was a rock and kelp reef, but it has since been inundated by silt from the Portuguese Bend landslide. As a result, its present condition is a sand/mud bottom with buried or sterile rock reefs. The habitat value of this site, 1188, closely approximates that of the combined soft substrate and water column at SONGS.

The kelp bed at San Onofre grows on a flat cobble bottom rather than a high relief reef. Based on surveys performed before the San Onofre Nuclear Generating Station began operations (Larson and DeMartini, 1984), the San Onofre kelp bed has a habitat value that is not much higher than that of the surrounding sand (1590 vs 1227). The value for the Palos Verdes reef, in contrast, is over three times as high (5754 vs 1590). If we use only the kelp transects from Palos Verdes, ignoring rock reef and cryptic fish data, the habitat value drops to 2950, which is still nearly twice the value of the San Onofre site. Decomposing an aggregate habitat value into individual components in this fashion may be one means of approaching a further analysis of comparison measures. The cryptic fish component of the Palos Verdes site, considered alone, generates a habitat value of 1622. This is almost identical to the habitat value of the cryptic fish component at the King Harbor site (1618), indicating some consistency in the results of decomposing the habitat values.

The Torrey Pines artificial reef, based on only eight months of comprehensive data from MEC, has the highest value of any habitat analyzed in our study (8659), including that of King Harbor artificial reef (4440), which is the most similar habitat among the primary sites. The "wetlands" sites are best represented by Allen's upper Newport Bay study, which lasted for 12 mo. Its value (4005) approaches the value of an artificial reef. The second wetland site, at Marina Del Rey, generated a much lower habitat value (2415). The difference was mainly attributable to lower densities in the Marina Del Rey survey; the number of species collected was comparable (or slightly higher) than was the case in Newport Bay.

Discussion

The results of the resampling analysis suggest that our guild-based method of habitat valuation is robust and efficient. It draws clean distinctions between habitat types, such as soft-substrate versus rock reefs, that are generally agreed to exhibit distinctive habitat values, but the valuation is to a large degree independent of which other comparison sites are selected. It is also relatively objective, in that it makes little use of expert judgement in determining the data to be included in the valuation. The technique can be employed using existing environmental surveys. If additional data are required, however, the measures used are sufficiently simple and straightforward that the costs of acquiring the data should not be burdensome.

Interpretation of the detailed results of our habitat valuation analysis is still, however, a fairly complex undertaking, mostly because of the difficulties of making use of existing data bases that employ diverse sampling methodologies. Perhaps the most important factor is the sampling interval. Fish assemblages can vary daily, seasonally, and annually, making it difficult to compare long-term, seasonally collected samples to samples taken at one season over several years or samples taken throughout the course of a single year. Figure 11 displays the habitat value of the King Harbor breakwater and the corresponding aggregate fish abundances over a decade of diver transects and cryptic fish surveys (1984–1993). The harbor reached its greatest estimated biomass in 1984 and its lowest point since 1975 in 1988 (Stephens et al., 1994). The habitat value is clearly buffered from fluctuations in aggregate abundance by the inclusion of components that are sensitive to diversity and fidelity, but our measure does track the changing trends in fish abundance. And the variation is still significant. The range in habitat value across years was 1875, nearly half of the long-term mean of 4362. Clearly, habitat values obtained from any single year will suffer a considerable reduction in accuracy.

Even very small differences in sampling techniques can also yield measurably different habitat valuations. For example, the VRG otter trawl data employed both 4.9 and 7.6 m headrope nets; other comparative surveys used only the larger net. The size of the net has a direct effect on catchability, especially of larger fish. Morris et al. (1996) recently documented a higher abundance of bat rays taken by California Department of Fish and Game with a large, 15 m otter trawl than with the smaller nets used by the VRG. Large, highly mobile fishes such as bat rays are particularly likely to be underrepresented in smaller cross-section trawls. Adams et al. (1995) compared surveys using a 29 m headrope trawl to video observations with a ROV; both methods gave much higher abundance values for the continental slope than the VRG otter trawls. Trawl data are also affected by the mesh

sizes of the trawl and the cod end. Most trawls from Southern California have used a standard cod end liner (0.5 in mesh), which retains a portion of immature or very small species. Data taken from nets with a larger cod end mesh will underestimate the contribution of smaller fish.

The habitat values obtained with the LACSD and SONGS data were considerably higher than those from comparable sites in the primary VRG data base. This may have resulted in part from just such subtle variations in sampling technique. Both of these comparison studies used only a 7.6 m net, which should have increased their take of large, mobile fish species. The VRG used both 4.9 and 7.6 m nets. Additionally, the vast majority of the trawls in the VRG data set were made during daylight hours, while the LACSD reported a six-fold increase in catch from trawls made at night (LACSD, 1981). The SONGS trawls were equally divided between diurnal and nocturnal sampling, and DeMartini and Allen (1984) conclude that the number and cumulative biomass of fishes caught at night was greater than during the day. The difference in sampling regime would, thus, also tend to produce a disparity in habitat value.

The decrease in habitat value with increased depth over soft bottom substrates (Fig. 7) is a conspicuous feature of our results. For benthic samples, both density and diversity of guilds declined significantly as depth increased. This effect is unlikely to be attributable solely to biases in sampling the water column. Because fishes in the sublittoral fringe are often widely distributed between the surface and the substrate, evaluation of shallow soft substrate habitats should generally include data from the water column, as well as the bottom fauna. The value of the shallow sand habitat is, thus, best estimated by the combined SONGS lampara and trawl data; the primary VRG shallow sand site was surveyed only with otter trawls, resulting in an unrealistically lower habitat value. The contribution of the water column to the habitat value of deeper sites is probably negligible, however. Although deep water trawls do not include the mesopelagic fauna that would increase the diversity of the sample, these habitats are dominated at mid-depths by schooling species and nonresidents, which have a much more variable seasonal and annual distribution on the open coast. The lower fidelities for these species would minimize their contribution to the habitat value measure, suggesting that the available trawl data is probably an adequate comparative survey of deeper soft-bottom habitats.

This relationship between depth and habitat value was not displayed in an earlier study, which found no evidence of a linear decrease in abundance with depth (Stephens et al., 1973). In fact, the deepest (>200 m) and shallowest (<10 m) trawls in these surveys apparently yielded about the same number of fish per trawl, with greater numbers in deeper shelf samples (100–200 m). The difference seems to have resulted from a lack of accurate estimates of bottom fishing time in the older literature. Our tests with a time-depth recorder have shown that actual bottom times in deeper water are as much as three times longer than those estimated by the fishing vessel, which would result in an unrealistically high estimate of both abundance and diversity for samples from the continental slope.

The greatly enhanced habitat values exhibited on some hard substrates are probably realistic. There is no doubt, however, that the use of different survey techniques—trawls on the soft-bottom sites and diver transects on the reefs—makes it difficult to obtain a precise estimate of the magnitude of the difference. Several studies have attempted to compensate for inefficiencies in sampling methods by adding a correction estimate (Stephens, 1978; MEC, 1988). Trawls are considered to have efficiencies of between 30 and 50%, and our estimates of density in the soft bottom sites could be adjusted accord-

ingly. At the same time, however, Davis and Anderson (1989) suggest that diver counts underestimate fish abundance by as much as 50 to 85%. As each method appears to underestimate abundance, and by roughly the same order of magnitude, it is not clear that introducing estimated corrections would significantly increase the reliability of the results. And the size of the difference in habitat values is far larger than would be expected on the basis of differences in sampling methods alone.

Environmental changes clearly have an impact on habitat value, but only when the damage to the habitat is extreme. For example, the burial of the kelp reef at Portuguese Bend under soft sediment resulted in the loss of kelp and the characteristic epibiota of hard substrates, changing the character of the habitat from a very productive reef to an average soft substrate site with only about one-fourth of the value of the Palos Verdes kelp reef. In this case, the damage was extreme, and the impact on the environment was apparent even with our aggregate measure. Furthermore, environmental degradation can also impact habitat value. For example, the habitat value of the SONGS kelp bed after plant startup probably accurately reflects the loss of kelp and its associated fish assemblage. In the case of the sewage outfall off White's Point, however, there is no apparent difference between the value of the comparable continental shelf sites and the outfall. In the VRG data sets, two guilds (guild numbers 9 and 20) are missing at the outfall, but both are only weakly represented in trawl data from the shelf, and both occur in the LACSD trawl data for the outfall site. Neither the density nor the diversity of fish species at the outfall appears to differ from that on the surrounding continental shelf. The apparent lack of impact may reflect the fact that neither of the trawl studies sampled exclusively from the zone of initial dilution around the outfall itself, an area which might be expected to show a substantial decrease in habitat value (Cross et al., 1985). Instead, most of the trawls at this site sampled areas adjacent to the outfall, which may well have represented ecotones that were enriched by the deposition of sewage. Unless the depositional material is acutely toxic, precluding biotic invasion, sewage deposits often seem to attract fishes.

The contrasts in apparent habitat value among the hard-substrate sites may reflect real environmental differences, but we are inclined to be cautious in making this interpretation. The studies from which the data were drawn were quite variable in methodology and timing, and it is not clear how much such differences contributed to the differences in the aggregate measure of habitat value. The SONGS kelp bed data, for example, were based on the Larson and DeMartini (1984) study, which did not include all species present at the site. They list only 24 species from the site, a much lower number than any comparable study. The VRG species list for King Harbor included 120 species, the Palos Verdes data showed 66 species, and both Ebeling et al.'s (1980) study of Naples Reef and the survey of Torrey Pines list 46 species. Without information on all species occupying the site, the SONGS data base probably underrepresents the number of guilds present, yielding a substantially lower habitat value.

There are, however, grounds to suppose that some aspects of the low habitat values for San Onofre may be fairly realistic. The habitat value resulting from the Larson and DeMartini data at San Onofre (1589) is surprisingly close to that produced by the combination of Allen and DeMartini's two studies of shallow soft bottom species (1227). The species and guilds in the two habitats are generally dissimilar, but the aggregate fish density is virtually the same. MEC reports a density of 54 1000 m^{-2} from the open coast shallow sand, which is identical to Larson and DeMartini's figure (56 fish 1000 m^{-2}) for cobble lacking kelp. Such a correspondence between two level habitats with disparate

substrate types suggests that the nature of the substrate has only a minimal influence on the habitat value.

The addition of kelp clearly has a major effect on habitat value, but most of the difference between San Onofre and the Palos Verdes site is probably attributable to the much greater relief in the latter habitat. With kelp present, Larson and DeMartini report a density of fishes at San Onofre of between 404 and 482 1000 m^{-2}, about eight times the density calculated from benthic sand or cobble bottom alone. DeMartini et al.'s (1989) survey conducted after the SONGS startup cites a comparable fish density in the remaining San Onofre kelp bed, roughly 450 1000 m^{-2}. By contrast, the VRG estimate of fish density in the kelp canopy alone at Palos Verdes (1981–1983) was much higher, 1096 1000 m^{-2}, and the high relief rocky substrate at that site yielded a density of 377 1000 m^{-2}, also much higher than the SONGS cobble substrate.

To quantify the contribution of small cryptic fish to the habitat value of a reef site, rotenone or quinaldine samples from known areas must be taken. At Torrey Pines divers swam special transects, searching for young of the year and other cryptic fishes. Such techniques overlook cryptic species that tend to hide in crevices, however. We have developed estimates for cryptic fishes for both King Harbor and Palos Verdes. Densities of these species at King Harbor exceed 4000 1000 m^{-2}; at Palos Verdes, they are greater than 5500. Allen et al. (1992) estimated about 2830 1000 m^{-2} at Catalina Island. They suggested that the density of cryptic fish at that site was four times that of conspicuous fishes observed in visual transects. Our estimates suggest the differential is at least that great. Any habitat value obtained for a hard-substrate site that lacks data from cryptic fish will be seriously underestimated.

Cryptic fish are, however, almost entirely restricted to three of the 23 guilds, totaling only about a dozen species, and are generally small in size. As a result, their contribution to our guild-based estimate of habitat value is lower than might be expected. Cryptic fish accounted for 28% of the value of the Palos Verdes habitat and 38% of that for King Harbor. If we use a 30% contribution as a "rule of thumb" for other habitats, the habitat value for the San Onofre kelp bed would be increased to 2065 by the addition of cryptic species. With this adjustment, the relative valuation of hard-bottom to soft-bottom habitats and the effect of bottom topography is clarified. Using the aggregate habitat value ratio from our long-term data sets, the King Harbor artificial reef is 3.6 times as valuable as shallow sand (using DeMartini and Allen's lampara + trawl data), and the Palos Verdes high relief rock reef/kelp bed is 4.2 times as valuable. Adding a 30% contribution of cryptic fish to the San Onofre low relief kelp bed, this site is only 1.7 times as valuable. These ratios appear to be reasonable estimates of comparative habitat values for the Southern California Bight.

The high values for the Torrey Pines artificial reef are something of an anomaly, as there is no auxiliary evidence that Torrey Pines is unusual for a Southern California reef in either density or species diversity. Ambrose and Swarbrick (1989) list species density, richness, and diversity on a series of natural and artificial reefs based on single sampling days. In these data, the Torrey Pines reef ranks second to Pendleton artificial reef in northern San Diego County, while King Harbor breakwater ranks third in fish abundance. Their estimate of richness and diversity at the Torrey Pines site is low compared to other areas. The intense study of this small reef (0.18 ha) reported 46 species on or adjacent to the reef, including six cryptic species, 25 observed during diver transects on the reef, and 14 noted in the adjacent sand or sand/rock ecotone. Considering the small area encom-

passed by the reef, this would appear to be only an average richness. Their estimate of fish density of 595 1000 m^{-2} is half as high as DeMartini et al.'s (1989) estimate for Pendleton artificial reef (1200 1000 m^{-2}) but higher than their estimate for the SONGS kelp bed. The VRG aggregate estimate of mean fish density for twenty years of data at Palos Verdes kelp, excluding cryptic fish, is 1471 1000 m^{-2} and for King Harbor breakwater is 742. These densities clearly exceed those of Torrey Pines artificial reef.

Within this study, all habitats represent areas greater than a hectare with the exception of Torrey Pines Reef. This reef 's area is only 0.18 ha and therefore, the calculated densities are multiplied by a correction factor to bring the reef area up to the standardized comparison value (1 ha). In this process, the habitat achieves a numeric value that far exceeds the actual value of this small reef. In order to reduce this value to its appropriate level, we must consider the entire hectare in which the reef exists. Torrey Pines reef is surrounded by sandy substrate. The reef itself has a value of 8659.7* 0.18 = 1559. The value of this substrate is considerably less than that of the reef. Surrounding the reef is an area 13 m in width that includes an enhanced fish assemblage due to reef influence. Based on the recorded fish density in this area of influence, the value of that substrate (0.246 ha) is 533. The remaining area of the hectare is sandy substrate uninfluenced by the reef. This area (0.574 ha) is valued at 497. The value of the hectare is equal to the sum of its elements or 1559 + 533 + 497 = 2589. DeMartini et al (1989) emphasize the importance of habitat are in discussing relative worth. When comparing habitats with areas less than the standard hectare, this technique will avoid habitat value inflation.

Conclusions

The results show that by making use of commonly collected data on fish populations, we can derive robust, objective, and quantitative comparisons between different types of marine and estuarine habitats. Other components of the aquatic community could, of course, serve as well for this purpose. Fish provide a central linkage in any analysis of marine food webs, however, suggesting that these organisms provide a common currency that can suffice as a reasonable and cost-effective measure of habitat value across a wide range of habitats. The strength of our methodology lies in its applicability to current data bases and standard monitoring techniques. For the Southern California Bight, our analysis is the most comprehensive that has ever been conducted and is clearly of immediate value to the interpretation of habitat differences in this ecosystem. In addition, because the three measures—mean length, fidelity and density—are almost invariably recorded in some form in any general survey of the fish fauna of a given area, our method can be applied to any similar region that has been repeatedly surveyed over a sufficient period of time.

The fish guild method should also assist the emerging field of restoration ecology. Legal requirements now often specify that habitat must be restored or newly created in compensation and mitigation for past or anticipated environmental damages. In many cases, however, restoration options at the impacted site may be limited, and the mitigation may involve recovery or generation of a different type of habitat at a separate location. To obtain an equivalence between the habitat that was lost or destroyed and that which is proposed in compensation, there must be a consistent, objective means of determining the relative value of the two sites. Because it is fairly free of subjective biases and inde-

pendent of which habitats are included in the analysis, the fish guild method will facilitate such habitat trade-offs and will insure better quantification of habitat sites that require mitigation. In addition, the guild-based values are readily interpretable, allowing informed decisions based upon solid scientific knowledge. We acknowledge that other factors (i.e. endangered species, endangered habitats, fisheries species, pollution, etc.) are important in determining habitat quality. However, we chose not to subjectively weight the model according to the desires of particular constituencies or user groups.

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APPENDIX A. GUILD CLASSIFICATION USED FOR HABITAT VALUATION

I. Water column

Guild 1: water column foragers, schooling, filter feeding
Threadfin shad (*Dorosoma petenense*), northern anchovy (*Engraulis mordax*), deepbody anchovy (*Anchoa compressa*), slough anchovy (*A. delicatissima*), Pacific sardine (*Sardinops sagax*).

Guild 2: selective feeding, diurnal
Mosquitofish (*Gambusia affinis*, specialized neustonic), grunion (*Leuresthes tenuis*), queenfish (*Seriphus politus*) <100 mm SL, walleye surfperch (*Hyperprosopon argenteum*) <60 mm SL, topsmelt (*Atherinops affinis*) <100 mm SL, white croaker (*Genyonemus lineatus*) <100 mm SL.

Guild 3: nocturnal
Queenfish (*Seriphus politus*) >100 mm SL, walleye surfperch (*Hyperprosopon argenteum*) >60 mm SL, salema (*Xenistius californiensis*).

Guild 4: benthic foragers, schooling, diurnal herbivores
Topsmelt (*Atherinops affinis*) >100 mm SL, striped mullet (*Mugil cephalus*, specialized detritus ingestor).

Guild 23: pelagic mesocarnivores
Pacific bonito (*Sarda chilensis*), Pacific mackerel (*Scomber japonicus*), California barracuda (*Sphyraena argentea*), spiny dogfish (*Squalus acanthias*), California needlefish (*Strongylura exilis*), jack mackerel (*Trachurus symmetricus*).

II. Substrate associated

Guild 5: w.c. foragers, schooling, selective feeding, usually benthic refugers, diurnal
Blacksmith (*Chromis punctipinnis*), señorita (*Oxyjulis californica*) <60 mm SL, calico rockfish

(*Sebastes dalli*) <100 mm SL, olive rockfish (*S. serranoides*) <60 mm SL, stripetail rockfish (*S. saxicola*) <100 mm SL, blue rockfish (*S. mystinus*).

Guild 6: nocturnal, visual
Stripetail rockfish (*Sebastes saxicola*) >100 mm SL, olive rockfish (*S. serranoides*) >60 mm SL, splitnose rockfish (*S. diploproa*).

Guild 7: non-schooling, non-visual
Specklefin midshipman (*Porichthys myriaster*), plainfin midshipman (*P. notatus*).

Guild 8: w.c./benthic foragers, schooling, often benthic refuging, diurnal, pickers
California killifish (*Fundulus parvipinnis*), señorita (*Oxyjulis californica*) >100 mm SL, kelp surfperch (*Brachyistius frenatus*), shiner surfperch (*Cymatogaster aggregata*).

Guild 9: non-schooling, diurnal, engulfers
Kelp bass (*Paralabrax clathratus*), spotted sand bass (*P. maculatofasciatus*), barred sand bass (*P. nebulifer*), giant kelpfish (*Heterostichus rostratus*), sablefish (*Anaplopoma fimbria*), bonefish (*Albula vulpes*).

Guild 10: nocturnal
California scorpionfish (*Scorpaena guttata*), calico rockfish (*Sebastes dalli*) >100 mm SL, kelp rockfish (*S. atrovirens*), shortspine thornyhead (*Sebastolobus alascanus*).

Guild 11: benthic foragers, schooling/non schooling, diurnal, generalists
Black surfperch (*Embiotoca jacksoni*), rainbow surfperch (*Hypsurus caryi*), dwarf surfperch (*Micrometrus minimus*), white surfperch (*Phanerodon furcatus*), pink surfperch (*Zalembius rosaceus*), opaleye (*Girella nigricans*) <100 mm SL, garibaldi (*Hypsypops rubicundus*, specialist, territorial, sometimes herbivore).

Guild 12: crushers
Rock wrasse (*Halichoeres semicinctus*), California sheephead (*Semicossyphus pulcher*), pile surfperch (*Rhacochilus vacca*).

Guild 13: herbivores
Opaleye (*Girella nigricans*) >100 mm SL, halfmoon (*Medialuna californiensis*), zebraperch (*Hermosilla azurea*).

Guild 14: nocturnal, generalists
White croaker (*Genyonemus lineatus*) >100 mm SL, black croaker (*Cheilotrema saturnum*), California corbina (*Menticirrhus undulatus*), yellowfin croaker (*Umbrina roncador*), rubberlip surfperch (*Rhacochilus toxotes*), sargo (*Anisotremus davidsoni*) (some crushing).

Guild 15: burrowers
Spotted cusk-eel (*Chilara taylori*), basketweave cusk-eel (*Ophidion scrippsae*).
III. Benthic

Guild 16: w.c./benthic foragers, mesocarnivores
Bigmouth sole (*Hippoglossina stomata*), California halibut (*Paralichthys californicus*), California lizardfish (*Synodus lucioceps*), cabezon (*Scorpaenichthys marmoratus*).

Guild 17: substrate sitters, microcarnivores, diurnal
Pacific sanddab (*Citharichthys sordidus*), speckled sanddab (*C. stigmaeus*), longfin sanddab (*C. xanthostigma*), slender sole (*Eopsetta exilis*), painted greenling (*Oxylebius pictus*), shortspine

combfish (*Zaniolepis frenata*).

Guild 18: nocturnal
Longjaw mudsucker (*Gillichthys mirabilis*), Pacific staghorn sculpin (*Leptocottus armatus*), snubnose sculpin (*Orthonopias triacis*), roughcheek sculpin (*Ruscarius creaseri*), blacktip poacher (*Xeneretmus latifrons*).

Guild 19: hiders (in holes and crevices), diurnal
Arrow goby (*Clevelandia ios*), cheekspot goby (*Ilypnus gilberti*), shadow goby (*Quietula y-cauda*), mussel blenny (*Hypsoblennius jenkinsi*), bay blenny (*H. gentilis*), reef finspot (*Paraclinus integripinnis*), bluebanded goby (*Lythrypnus dalli*), zebra goby (*L. zebra*), yellowfin goby (*Acanthogobius flavimanus*), blackeye goby (*Coryphopterus nicholsii*), bay goby (*Lepidogobius lepidus*).

Guild 20: benthic foragers, pickers and scrapers, diurnal
Spotted kelpfish (*Gibbonsia elegans*), stripefin ronquil (*Rathbunella hypoplecta*), rockpool blenny (*Hypsoblennius gilberti*).

Guild 21: nocturnal, non-visual
California tonguefish (*Symphurus atricauda*), rex sole (*Errex zachirus*).

Guild 22: diggers and extractors
Diamond turbot (*Hypsopsetta guttulata*), bigfin eelpout (*Lycodes cortezianus*), blackbelly eelpout (*Lycodes pacifica*), c-o turbot (*Pleuronichthys coenosus*), spotted turbot (*P. ritteri*), hornyhead turbot (*P. verticalis*), Dover sole (*Microstomus pacificus*), English sole (*Pleuronectes vetulus*), round stingray (*Urolophus halleri*).